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Ameztegui A, Coll L (2013) Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. Forest Ecology and Management 303: 25-34. DOI: https://doi.org/10.1016/j.foreco.2013.04.011

Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients

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ABSTRACT

The predicted upward displacement of forest species due to climate warming is expected to be modulated by a medley of abiotic and biotic factors acting at microsite level. Species-specific differences in plant responses to this set of environmental factors can thus have strong implications in the future dynamics of forest ecosystems. To gain a better understanding of the main fine-scale factors and processes driving present and future species performance in the montane and subalpine belt of the Eastern Pyrenees (NE Spain), we established a set of experimental mixed plantations along elevational and environmental gradients using the four tree species dominating these areas (*Pinus sylvestris*, *Pinus uncinata*, *Abies alba* and *Betula pendula*). Once the plantations had been established, the performance and growth of 72 seedlings of each species was monitored and linear and non-linear models were fitted to identify the main factors controlling their survival and growth.

We found most of the mortality to occur during the third growing season, following a harsh winter and a drought period during summer. Mortality patterns were highly species- and site-specific. At the subalpine belt, shrubs were found to have a facilitative effect on winter survival of *P. sylvestris* (mortality < 10%) but not on the other species. At the montane belt, *A. alba* mortality during the summer increased in areas with high light exposure and herbaceous cover (mortality > 30%). All species except *P. uncinata* showed lower height growth at high elevation, with differences between sites matching differences in growing season duration (20%).

Our results underline the strong impact that short periods of extreme climate can have in the performance of plants developing in mountainous areas far from their optimal elevational range. However, they also underline a potentially critical role played by biotic and abiotic microsite factors in mediating species responses to these climatic events.

Keywords: Seedlings, plant-plant interactions, elevational gradient, climate change, Pyrenees, facilitation

1. INTRODUCTION

The predicted increase in temperatures caused by global warming (IPCC, 2007) is expected to have large effects on mountain ecosystems, where the elevational ranges of trees are mainly controlled by temperature (Grabherr et al., 1994; Walther et al., 2002; Peñuelas and Boada, 2003; Lenoir et al., 2008). Accordingly, most simulations based on 'climate envelopes' predict upward or poleward displacement of species under future warming scenarios (Guisan et al., 1998; Dullinger et al., 2004), with some species even becoming extinct if the rate of change exceeds their pace of biological response (Thomas et al., 2004; Thuiller et al., 2005). However, realized ecological niches are multidimensional, and species distribution is not only explained by macro-climate but also by species-specific responses to a medley of abiotic and biotic factors that often operate at finer temporal and spatial scales (Vetaas, 2002; Walther et al., 2002; Dullinger et al., 2004; Holtmeier and Broll, 2005). The effects of these factors are often not adequately captured by the 'climate envelope' models (Ackerly et al., 2010; Scherrer and Körner, 2011), sometimes leading to unrealistic predictions of species distributional changes (Randin et al., 2009; Willis and Bhagwat, 2009; Martínez et al., 2012).

In many mountain ecosystems, abiotic stresses are considered the major mechanism setting the upper limit of species' elevational ranges. To successfully migrate upwards, tree species must be able to grow and survive outside their current elevational range, thus facing climatic conditions that are at the limits of their physiological tolerance (Lenoir et al., 2009; Lenoir et al., 2010), particularly at their younger stages (Germino et al., 2002; Gómez-Aparicio et al., 2008a). Therefore, in these areas, short periods of extreme climatic conditions (e.g. extreme cold or freezing events) play a critical role in shaping future species composition (Schneider, 2004; Lindner et al., 2010). However, some recent studies have shown that micro-topographical factors can buffer or even override the effects of harsh climate on plant survival (Ackerly et al., 2010; Scherrer and Körner, 2011). Positive plant-plant interactions could also play a major role in these stressful environments, as postulated by the 'stress-gradient hypothesis' (SGH; (Bertness and Callaway, 1994; Maestre et al., 2009). Shrubs for example are known to facilitate the survival of young plants of species growing at their upper elevational limit by reducing wind abrasion, mitigating the minimum temperatures to which they are exposed, protecting them from radiation, or reducing snowdrift (Batllori et al., 2009; Barbeito et al., 2012).

Conversely, competitive effects are considered the major mechanism setting the lower limit of species' elevational ranges (Lenoir et al., 2010). However, this might not occur when

environmental severity increases at low elevation. In such cases, species' sensitivity to the main stress factor (e.g. drought in Mediterranean mountains) would significantly define its lower range margin (Macias et al., 2006; Candel-Pérez et al., 2012; Linares and Camarero, 2012). Other processes not directly related to climate, such as habitat modification due to changes in human activities have led to severe canopy closure in many European forests (Poyatos et al., 2003; Ameztegui et al., 2010), which can also induce significant shifts in species distribution, even favoring downslope displacement of some shade-tolerant species (Lenoir et al., 2010; Bodin et al., 2013).

In the Pyrenees, the rise in temperatures associated to climate change has prompted predictions of species displacements (Resco et al. 2006) with a progressive upward encroachment of montane species into the subalpine belt (Ameztegui and Coll 2011). However, these areas are characterized by a high variability of abiotic and biotic factors acting at local scale, whose role in these apparently climate-driven processes remains unclear. With the ultimate aim of advancing understanding of the relative impact of these factors in the future dynamics of the Pyrenean mountainous forests, we set up a 4-year field experiment in which seedlings of the 4 most widespread tree species in the montane and subalpine belt of the Eastern Pyrenees (*Pinus sylvestris* L., *Pinus uncinata* Ram, *Abies alba* Mill. and *Betula pendula* Roth.) were planted along gradients of elevation and microsite conditions (light availability and herbaceous and shrub cover). Specifically, we aimed to answer the following questions: i) how does the performance (survival and growth) of these species vary along environmental gradients including variation in climate, light availability and biotic interactions?; ii) what role do short extreme climatic events play in seedling survival and growth?; iii) are the intensity and sign of biotic interactions (competitive vs. facilitative) species-specific?; and iv) can plant-plant interactions favor or limit species range expansion by modulating the effects of climate change through facilitation and competition?

We hypothesized that climate (minimum temperatures at high elevation and drought at low elevation) would play a determinant role in seedling mortality, but that biotic interactions could partially buffer this effect, especially for those species established far from their optimal elevational range.

2. METHODS

2.1. Study area

The experiment was conducted at two different elevations in the northern slopes of the Serra del Cadí, a Pyrenean mountain range in the Cadí-Moixerò Natural Park (42º17' N; 1º42' E). The "low-elevation" plots were located in the montane belt, slightly below the *P. sylvestris–P. uncinata* transition zone (around 1500 m a.s.l.). The forest overstory in this site was dominated by *P. sylvestris* (more than 75% of total basal area) with some *P. uncinata* and *B. pendula* individuals, whereas the main species in the understory were common box (*Buxus sempervirens* L.) and common juniper (*Juniperus communis* L.). The "high-elevation" plots were located in the subalpine belt (around 2000 m a.s.l.), close to the optimum elevational distribution for *P. uncinata*. In this site, the overstory was overwhelmingly dominated by *P. uncinata*, although some disperse individuals of *A. alba* and *B. pendula* could be found. The shrub layer was almost exclusively composed by *J. communis*. These two areas (located in the same valley but set 12 km apart) present contrasting climates associated to the abrupt terrain involving marked elevational zonation of the vegetation (Ninot et al., 2007).

2.2. Species selection and characteristics

This study focused on the 4 most widespread tree species in the area: Scots pine (*P. sylvestris*), a shade-intolerant species that in the Pyrenees can be found between 1000 and 1800 m a.s.l., thus dominating the montane belt of the Pyrenees; mountain pine (*P. uncinata*), a shade-intolerant conifer that reaches its southern distributional limit in the Iberian Peninsula and constitutes most of the treelines in the Pyrenees as it is restricted to the subalpine belt (between 1600 and 2300 m a.s.l.); silver fir (*A. alba*), the most shade-tolerant conifer species in the Pyrenees, usually restricted to humid sites on north-facing, shady slopes between 1200 and 2000 m a.s.l. where the risk of water stress in summer is lower (Macias et al., 2006); and silver birch (*B. pendula*), a shade-intolerant pioneer species that usually colonizes disturbed areas between 1000 and 1800 m a.s.l. but only rarely reaches the canopy (Ruiz de la Torre, 2006). These species differ in their ecological requirements, and they can be ordered from most (rank=5) to least (rank=1) shade tolerant following the ranking system developed by Niinemets and Valladares (2006): *A. alba* (4.6 ± 0.06; mean ± SE), *B.pendula* (2.03 ± 0.09), *P. sylvestris* (1.67 ± 0.33), and *P. uncinata* (1.2). Moreover, the drought tolerance ranking order according to the same authors would be: *P. sylvestris* (4.34 ± 0.47); *P. uncinata* (3.88), *B. pendula* (1.85 ± 0.21) and *A. alba* (1.81 ± 0.28). Despite their different ecological requirements, these four species are

able to coexist in a strip between 1600 and 2000 m a.s.l. constituting the local montane-subalpine mixed forest.

2.3. Experimental design

At each one of the two sites, 72 two-year-old seedlings of each of the 4 studied species were distributed into 12 plots and planted in early summer 2008. Plot size varied between 40 and 50 m² and each plot included 24 seedlings (6 per species) planted at least one meter apart to avoid interaction between them. Half of the plots were located in the forest understory and the other half in naturally-occurring gaps (Figure 1). Gap surface was between 150 and 350 m² (196.0 ± 33.4 m²; mean ± SE). Seedlings were randomly distributed across each plot, and were carefully planted to minimize alteration of the micro-environment. As domestic herds of cattle and horses are led into these forests during the summer, the seedlings were protected from browsing with an individual protector (90 cm height and 33 cm of diameter) with a 20 x 20 mm mesh net (Nortène, Lille, France) to exclude the influence of animal damage. All the seedlings were 2 years old at the time of planting and had been grown in a local nursery (Forestal Catalana, Pobla de Lillet, Spain) from seeds collected in neighboring forests. For all species, seedling source, nursery and plantation area were all inside the same region of provenance (Alía et al., 2005).

2.4. Characterization of the environment and explanatory variables

To better characterize climatic differences between the two sites, two meteorological stations were installed (one per site), and air temperature (at 1 m height), below-ground soil temperature (at 10 cm depth) and precipitation were measured continuously using ECH2O sensors (Decagon Devices, Pullman, WA, USA; see Table 1). Data from the *in situ* meteorological stations registered high climatic variability over the 4 years of the study. In August and early September 2011, there was a rather warm and dry period (with 60% less precipitation than the average for the last 10 years, Figure 2) that exposed the vegetation to a significant drought stress that was visually appreciable even in the adult stand. The winters of 2009 and 2010 were particularly cold, with minimum temperatures reaching -15.8ºC in the high-elevation sites. In early winter 2010, the cold period coincided with low precipitations, resulting in the shallowest snow layer seen in recent years (Figure 2).Throughout the duration of the study, the seedlings established at high elevation (subalpine sites) were exposed to lower mean temperatures, higher precipitations, higher Thornthwaite index and a 20% shorter growing period than the seedlings established at lower elevation (Table 1).

To characterize the microsite conditions of the planted seedlings, light availability, percentage of herbaceous cover and distance to nearest shrub were measured for each of the seedlings (Table 1). Light availability was measured using two Li-190SA quantum sensors (LI-COR, Lincoln, NE, USA). The sensors were used in paired mode, *i.e.* one of the sensors was placed at the top of each seedling and the other in an adjacent open area, following standard procedure (see Messier & Puttonen (1995) and Parent & Messier (1996) for a complete description of the method). This approach makes it possible to calculate light availability as a percentage of transmitted photosynthetic photon flux density (%PPFD), and consequently ranged from 0 (complete obstruction) to 100 (open sky). The measurements showed mean light availability to be slightly higher in the subalpine plantations, but the range was similar at both elevational sites, with a maximum of about 60% (Table 1). Percentage of herbaceous cover surrounding the seedlings was visually estimated to the nearest 5% using an 80 x 80 cm grid centered on each seedling, and was found to be higher overall at the subalpine belt (although extremely variable, with values ranging from 0 to 90-95% at both sites). Finally, distance from each seedling to the nearest shrub was measured with a tape meter. We defined a shrub as any woody plant with several stems arising from the base, so other elements such as neighbor seedlings, adult trees, logs or rocks were not considered. The montane sites showed higher shrub density, resulting in a lower mean distance of seedlings to the nearest shrub (Table 1).

2.5. Seedling monitoring

Seedling mortality was regularly monitored throughout the duration of the experiment. With the aim of disentangling the main climatic variables driving mortality for each species at each elevation, we divided the observed mortality into either summer mortality (occurring during the growing season) or winter mortality (occurring during the winter). The plots were frequently visited, and we only assigned mortality to a given period (summer or winter) when plants were found to be dead in the beginning of a period but had been recorded as healthy (absence of any symptom of disease) at the end of the previous one. Despite the protective net, seven seedlings were damaged by animals, mainly by trampling, and were subsequently excluded from the analysis. Furthermore, 13 seedlings died due to small disturbances (e.g. stones falling, small landslides…) and were also excluded, giving a total of 552 seedlings analyzed.

Seedling size was monitored by measuring total height and diameter at the root collar at the end of every growing season. Using this dataset, we determined the following response variables: 1) survival rate along the 39 months of the study; 2) winter and summer mortality; 3) height at the end of the study period; and 4) diameter at the end of the study period.

2.6. Data analyses

For each species and site (montane vs. subalpine), survival function curves were developed based on Kaplan-Meier estimates, and the Mantel-Cox log-rank test was used to determine significant differences between sites. To test the effect of categorical or continuous covariates on our censored survival data, we used a Mixed Effects Cox model (Therneau and Grambsch, 2000), which is a modification of the commonly used Cox's Proportional Hazards (coxPH) model (Cox, 1972) that allows for inclusion of random covariates. For each combination of response variable (summer and winter mortality) and species, we fitted a separate model in which the effects of the three explanatory variables at microsite level (herbaceous cover, distance to shrubs, and light availability) and elevation (site) were introduced as fixed factors, whereas plot was introduced as a random factor. The equation fitted by the model was:

$$\lambda(t) = \lambda_0(t)\, e^{X\beta+Zb}$$

$$b \sim G(0, \Sigma(\theta))$$

where $\lambda_0(t)$ is an unspecified baseline hazard function, X and Z are the design matrices for the fixed and random effects, respectively, β is the vector of fixed-effects coefficients, and b is the vector of random effects coefficients. When comparing two groups, the hazard ratio (e^{β}) is the quotient of the hazard functions for each of the groups. For a continuous variable, the hazard ratio indicates the change in the risk of mortality if the parameter in question rises by one unit. The random effects distribution G is modeled as Gaussian with mean zero and a variance matrix Σ, which in turn depends on a vector of parameters θ. To test the significance of each variable, we performed a likelihood ratio test (LRT) to compare deviances of a pair of nested models: a null model (in which the variable was absent) and an alternative model including it. Interactions between variables were only included if the LRT of the model indicated significant difference with both the simpler models. Goodness-of-fit of the models was assessed through the concordance statistic (C), which is analogous to Kendall's tau between the prediction and the outcome but can be used with censored data.

Several model formulations (linear, exponential, power and Michaelis-Menten; see Appendices for details on the model equations) were used to analyze the effect of the different explanatory variables (light availability, herbaceous cover and distance to nearest shrub) on seedling size (height and diameter) at the end of the study period (39 months). Initial seedling size was introduced as a covariate with an exponent α to allow for non-linear relationships between final

and initial size. The maximum likelihood parameter values were estimated using simulated annealing (Goffe et al., 1994) and the asymptotic 2-unit support intervals were used to assess the strength of evidence for individual maximum likelihood parameter estimates. The R^2 of the regression of observed *versus* predicted values provided a measure of the goodness-of-fit of each model, and alternative models were compared using ΔAICc, the difference in corrected Akaike information criterion (Burnham and Anderson, 2002). Following the likelihood approach, we used comparison of alternate models to test our hypotheses. For each explanatory variable, the best of the 4 formulations (linear, exponential, power and Michaelis-Menten) was compared (in terms of ΔAICc) to a null model in which there was no effect of the independent variable, and we considered that an effect of this variable was supported when ΔAICc> 2. When there was substantial support for more than one independent variable, we also tested a bivariate model in which both variables were included, and the strength of evidence for this model was compared with univariate models. Finally, when the best model had been identified, we also tested for an effect of elevation by comparing the strength of evidence of a model in which parameters were estimated separately for low- and high-elevation sites against another model in which all the data were pooled together, and we retained the first model only if it was substantially supported by the data (ΔAICc> 2).

All analyses were performed using R 2.14.1 software (R Development Core Team, 2011) and the 'likelihood' v. 1.5 (Murphy, 2012), 'survival' v. 2.37-2 (Therneau, 2011) and 'coxme' v.2.2-3 (Therneau, 2012) packages for R.

3. RESULTS

3.1. Seedling survival

Survival rate after three growing seasons was significantly different among species ($P < 0.001$) and ranged from more than 80% for *P. uncinata* to less than 65% for *P. sylvestris*. For the three conifer species (*A. alba*, *P. sylvestris* and *P. uncinata*), most of the mortality at both elevations (more than 60% of total dead seedlings) was observed during the third year. Between-site differences in survival rates were only significant for *P. sylvestris* ($P < 0.001$) and *A. alba* ($P = 0.044$; Figure 3). These species presented opposite patterns, with *P. sylvestris* showing higher mortality in subalpine sites and *A. alba* showing higher mortality in montane sites. The seasonal patterns of mortality were also species-specific. While most of the *P. uncinata* and *A. alba* mortality occurred during the growing season, for the other two species it occurred during the winter (Figure 3).

P. sylvestris was the only species that showed an effect of the explanatory variables on winter mortality. The winter mortality of *P. sylvestris* was found to be positively associated with elevation (hazard ratio [HR] = 4.13; 95% CI: 2.15 – 7.95; P < 0.001) and with seedling distance to the nearest shrub (HR = 1.004; 95% CI: 1.002 – 1.007; *P* < 0.001; Figure 4). At the subalpine belt, mortality rate for seedlings planted at less than 0.5 m from a shrub was 0.11, whereas mortality rate for the rest of the seedlings ranged between 0.28 and 0.44. The positive effect of the shrubs on winter survival was not as marked at the montane belt, where mortality rates ranged from 0 to 0.13, but we did not find a significant effect of the interaction between distance to nearest shrub and elevation (*P* = 0.112). For the other three species (*P. uncinata*, *B. pendula* and *A. alba*), we could not detect an effect of any of the explanatory variables (including elevation) on winter mortality (Appendix A).

A. alba was the only species that showed a significant effect of the analyzed abiotic and biotic factors on summer mortality. For *A. alba*, both herbaceous cover and light availability were positively associated with mortality. The analyses also revealed a significant correlation between both variables (Pearson correlation coefficient = 0.21 for the montane belt; 0.42 for the subalpine belt) and the bivariate model including them was not significantly better than the univariate models. Herbaceous cover showed the most significant effect on mortality (*P* < 0.001), and we found a significant interaction between this variable and site (*P* < 0.001): the effect of herbaceous cover on mortality was only significant at the montane belt, where the observed mortality rate ranged from 0.08 for low classes of herbaceous cover (< 20%) to 0.33 for seedlings planted in sites with more than 80% herbaceous cover (HR = 1.120; 95% CI: 1.047 – 1.198; *P* < 0.001; Figure 5). Light availability was also positively associated with a higher mortality rate (HR = 1.056; 95% CI: 1.017 – 1.097; *P* = 0.036), with a maximum of 0.25 for seedlings with more than 40% PPFD available, but without significant effect of elevation in this trend (*P* = 0.882; Figure 5). An effect of herbaceous cover in the mortality of *B. pendula* was also detected, although the model including this variable was only marginally significant compared to the null model (HR = 1.020; 95% CI: 0.998 – 1.043; *P* = 0.055; Appendix B).

3.2. Seedling growth

There were significant among-species differences in absolute height growth, which ranged from 15 $mm \cdot y^{-1}$ for *A. alba* to more than 70 $mm \cdot y^{-1}$ for *B. pendula* (Table 3). These differences were weaker when considering relative height growth, but *B. pendula* still had higher growth than both pines, which in turn grew faster in height than *A. alba*. All species showed higher relative height growth at low-elevation sites, but the differences were not significant for *P. uncinata (P*

= 0.73). In contrast, all species showed higher relative radial growth at the subalpine site, but the differences were only significant for the two pine species (Table 3). However, measured radial growth over the 3 years was rather low (annual relative radial growth < 0.1 mm for all species), and we discarded it from further analyses as these values were below the measurement accuracy.

Light availability was the main environmental factor controlling height of the three conifer species (*P. uncinata*, *P. sylvestris* and *A. alba)*. For *A. alba* and *P. sylvestris*, the effect of light availability on growth was modulated by elevation, with seedling growth showing lower response to enhanced light (or almost null response in the case of *A. alba*) at low elevation than at high elevation (Figure 6). For *A. alba*, the observed response was linear, whereas for *P. sylvestris* it followed a power equation (Table 2; Figure 6). These differences in response with elevation were not observed for *P. uncinata*, for which relative height growth increased with light availability but was saturated at %PPFD > 40%, following a Michaelis-Menten equation (Table 2; Figure 6). For these species, the exponent of the initial height (introduced as a covariate in the model) ranged between 0.4 and 0.6, thus indicating a non-linear relation between this variable and final height. In contrast, the relation between initial and final height growth was linear for *B.pendula* ($\alpha = 1.01$), which was the only species for which there was no detectable effect of microsite factors or elevation on height (Appendix C).

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4. DISCUSSION

Mortality events in the established plots took place at different periods of the year in the two studied elevations. At the subalpine belt, a majority of mortality occurred during winter, whereas at the montane belt a majority of mortality occurred during the growing season. Although mortality was relatively low for all species during the first two years after plantation, it sharply increased during the third year when the area was exposed to a particularly cold late-autumn and early-winter followed by a drought episode during summer. The potentially strong impact of short events of extreme climatic conditions on juvenile tree mortality has already been observed elsewhere (Schneider, 2004; Saccone et al., 2009; Lindner et al., 2010), and in our sites we observed marked species-specific responses to these events. The harsh winter particularly affected *P. sylvestris* plants growing in the subalpine belt, where this species ranked as the least adapted to the climatic conditions, whereas as expected, summer drought mainly affected *A. alba*, which is the least drought-tolerant of the four studied species. Interestingly, the negative effect of drought in *A. alba* survival was only observed in the montane sites.

Positive plant-plant interactions were found to be species-specific and to vary with elevation, being particularly important for the survival of species establishing at the extremes of their elevational range. This was the case for *P. sylvestris* seedlings, a species typical of the montane belt and consequently the least adapted to the harsh climate of the high-elevation plots. Our results agreed with the stress-gradient hypothesis (Bertness and Callaway, 1994) and are consistent with previous research showing facilitation to be more important for species planted at experimental sites located at higher elevations than their distributional mean (Batllori et al., 2009). Our results also stress the major role that facilitation could play in modulating the effects of extreme climatic events such the extremely cold late-autumn and winter of 2010 in our experimental sites (Brooker et al., 2008; Saccone et al., 2009). We did not find a facilitative effect of shrubs on *B. pendula, A. alba* or *P. uncinata* plants. For the first two species, this could be explained by the fact that they are less drought-tolerant than pines (in particular *A. alba*), and competition for water from the neighboring shrubs may probably overcome their positive nurse effect. As pointed out by Maestre et al. (2009), in extremely severe environmental conditions, resource uptake by facilitators can overcome their positive effect if the stress is resource-based and the beneficiary species are not stress-tolerant. The lack of facilitative effects of *P. uncinata* was not surprising, given that this species is the best adapted to climate at the subalpine belt and presented relatively low overall mortality over the course of the experiment.

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At the montane belt, most of the mortality occurred during summer and more specifically during the third year's growing season when the area was exposed to a major drought episode. This event mainly affected *A. alba,* a species well-known to be highly sensitive to water deficit, being negatively affected by high temperature conditions and the related drought stress (Rolland et al., 1999; Pagès et al., 2003; Peguero-Pina et al., 2007; Toromani et al., 2011). The positive effect of light closure on *A. alba* survival might indicate a facilitative effect of tree cover on *A. alba* seedlings by reducing the Vapor Pressure Deficit to which the seedlings were exposed and thus indirectly limiting the development of competitive herbaceous neighbors (Pagès et al., 2003; Saccone et al., 2009). This indirect facilitative effect of canopy cover seemed to be particularly important in our study sites given the marked negative relationship found between herbaceous cover and *A. alba* survival, that was probably associated to competition for water. The herbaceous cover also increased mortality of *B. pendula* in the montane belt, although this effect was only marginally significant. In general, *B. pendula* is considered to tolerate drought much better than *A. alba* but shows a lower ability to compete for water than pines (Prevosto and Balandier, 2007).

In the montane site, we expected to find a positive effect of shrubs on plant survival (at least for the most drought-sensitive species) after the marked drought period that occurred during the third growing season. In the drier areas of Mediterranean mountains, seedlings frequently benefit from habitat amelioration by shrubs which reduce the radiation and temperature to which they are exposed and thereby improve their water status (Castro et al., 2002; Castro et al., 2004; Gómez-Aparicio et al., 2004; Gómez-Aparicio et al., 2008b) However, we did not detect any positive effect of shrubs on plant survival, indicating that in this relatively mesic area, the net effect of the and negative interactions occurring above- and below-ground between the shrubs and the seedlings was neutral.

Interestingly, we did not observe a higher mortality of *P. uncinata* in the montane belt, where this species was planted below its current elevational range, and neither biotic nor abiotic factors exerted any influence on the rate of *P. uncinata* mortality. Although the lower limit of species' elevational ranges in Mediterranean mountains is often considered to be set by drought-induced stress (Macias et al., 2006; Candel-Pérez et al., 2012; Linares and Camarero, 2012), our results suggest that this might not be the case for *P. uncinata*. It is possible that the current low elevational limit of *P. uncinata* is not climatically-driven but is instead set by other factors, such

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as competitive interactions with low-elevation species, mainly *P. sylvestris* (Callaway et al., 2002; Ameztegui and Coll, 2011).

In contrast to the abovementioned species-specific and temporal patterns, all the species studied grew faster in height in the montane belt than in the subalpine belt. Growth is known to be mainly limited by duration of the growing season in high-elevation forests (Grace and Norton, 1990; Grace et al., 2002; Hoch and Körner, 2003; Cailleret and Davi, 2010). Here, the average reduction in growth (20%) found in *P. sylvestris, A. alba* and *B. pendula* seedlings matched the average difference in length of the growing season observed between both sites during the experiment (Table 3). In contrast, *P. uncinata* (the species currently dominating the subalpine belt) presented the same height growth-light relationship at both elevations, following the typical saturating curve for environments where light is the most limiting factor (Ameztegui and Coll, 2011). However, the height growth of all species increased with higher light availability, thus indicating that the microsite requirements for seedling survival were different from those required for growth, as observed in the Alps by Barbeito et al. (2012).

In summary, this study showed that short periods of extreme climate can have a strong impact on the mortality of species growing far from their mean elevational range (e.g. *P. sylvestris* in the subalpine belt; *A. alba* at the montane belt). We found that positive plant-plant interactions can play a critical role in mediating the effects of these unfavorable climate conditions on the performance of these species when growing above their current limits. In contrast, in the lower limit of species' elevational ranges, competition plays a more important role. Overall, we conclude that species-specific differences in performance under different environmental conditions and the role of plant-plant interactions should be explicitly considered when making predictions of climate change-induced species displacement and when designing or implementing management plans to contend with the impacts of climate change.

ACKNOWLEDGEMENTS

This research was primarily supported by the Spanish Ministry of Science and Innovation via the projects Consolider-Ingenio Montes (CSD2008-00040), DINAMIX (AGL2009-13270-C02) and RESILFOR (AGL2012-40039-C02-01). The Spanish Ministry of Science provided LC with support through a Ramon y Cajal contract (RYC-2009-04985), and the Spanish Ministry of

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Education provided AA with support through a predoctoral grant (FPU Program - AP2007-01663). The authors are particularly grateful to A. Bargués, S. Martín, L. Ivorra and M. Pallarés for their invaluable work during field sampling and laboratory processing. F. Cano helped us to find the most suitable forests for this study, and the Socarrel team kindly offered their facilities during the fieldwork stage. We also thank the 'Parc Natural del Cadí-Moixeró' and the 'Montellà i Martinet' municipality for kindly giving permission to access the park and sample the data. Three anonymous reviewers provided helpful comments and suggestions.

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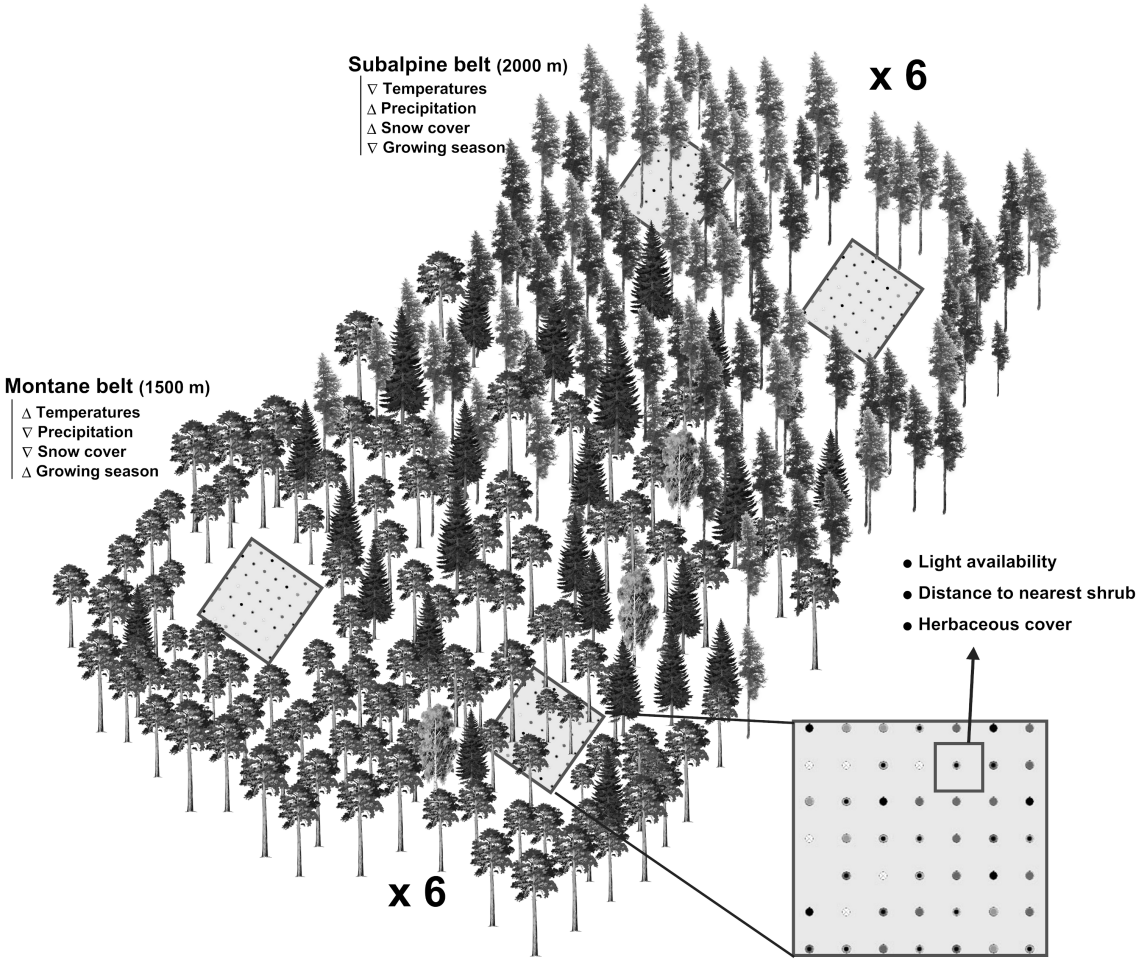

Figure 1.Representation of the experimental design and the measured abiotic and biotic variables. At each of the two sites (montane and subalpine belt), 6 plots were located in the forest understory and 6 in naturally-occurring gaps. At each plot, 24 seedlings (6 per species) were planted, and environmental variables at the microsite scale (light availability, herbaceous cover, and distance to nearest shrub) were measured.

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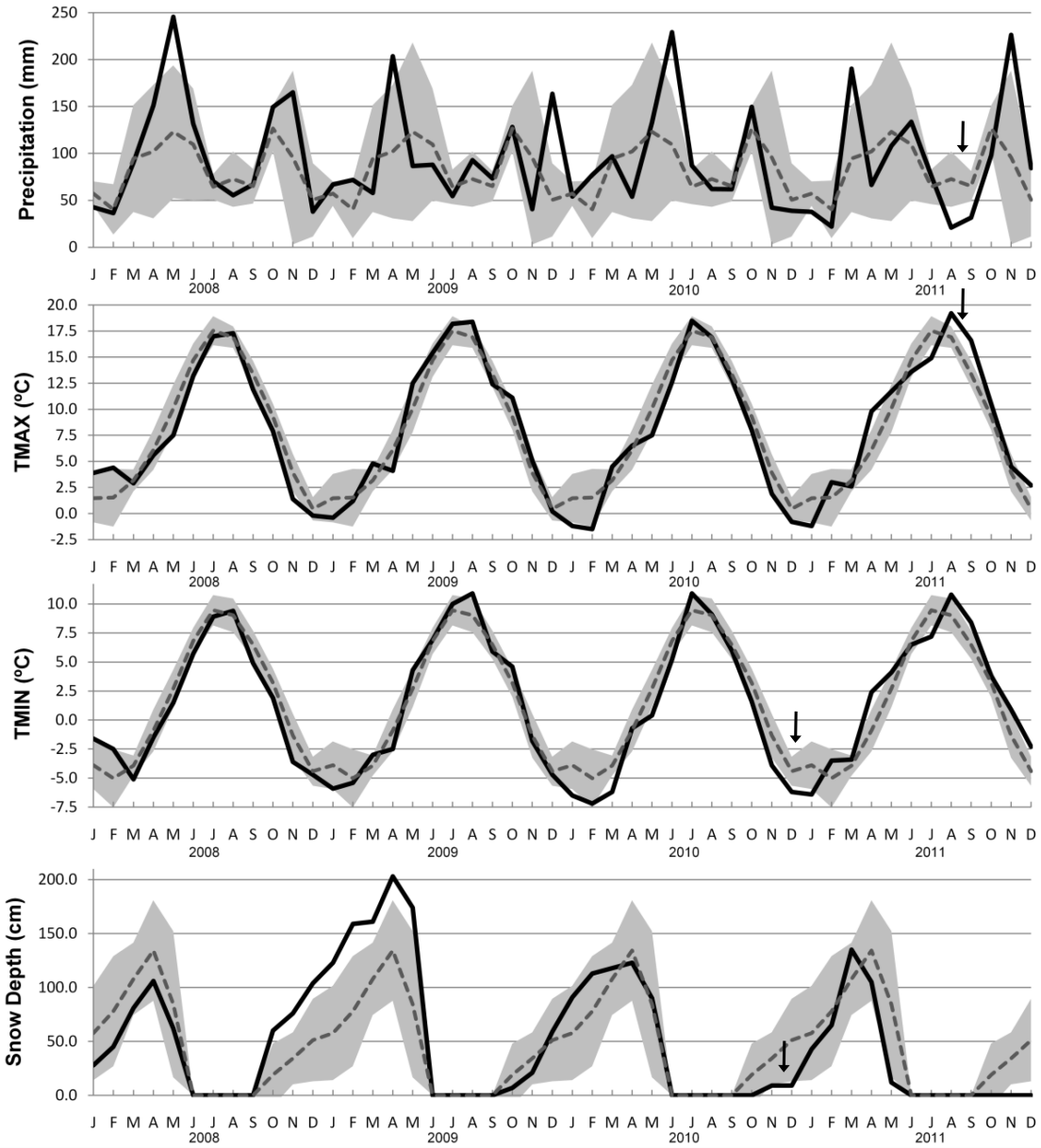

Figure 2. Evolution of precipitation, monthly average of the maximum (TMAX) and minimum (TMIN) temperatures and snow depth in the study area over the four-year study period (2008-2011). Dashed lines and shaded areas indicate mean ± SD during the last 10 years, whereas solid lines indicate measured values. Data are from the Prat d'Aguiló meteorological station (2138 m a.s.l.), located less than 1 km away from the high-elevation site. Vertical arrows indicate the extreme climatic events that occurred during late-autumn 2010 and summer 2011 (see text for further details).

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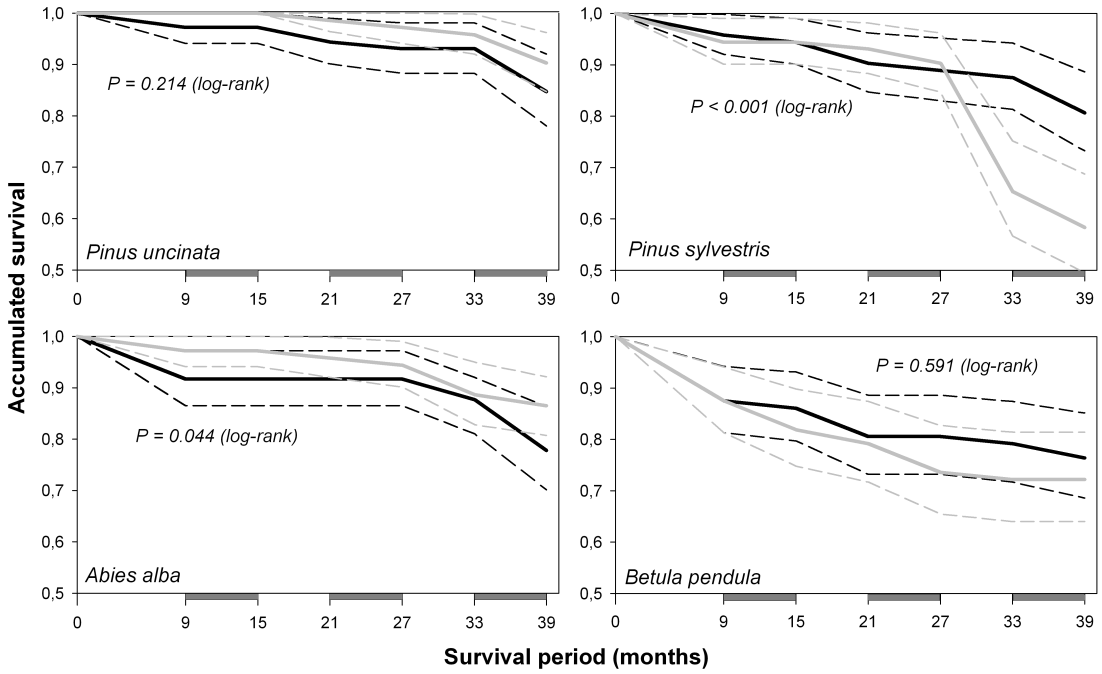

Figure 3. Survival curves for seedlings of the four species of trees planted at the two experimental sites over the course of the study period, based on Kaplan-Meier estimates. Black and grey lines represent seedlings in the montane and subalpine belts, respectively. Solid lines represent Kaplan-Meier estimates whereas dashed lines are 95% confidence intervals. *P*-values indicate significance of the log-rank test between sites for each species. Shaded areas in the x-axis correspond to the vegetative period (from May to October). Note that the *y*-axis starts at 0.5 for greater clarity and easier comparison among species.

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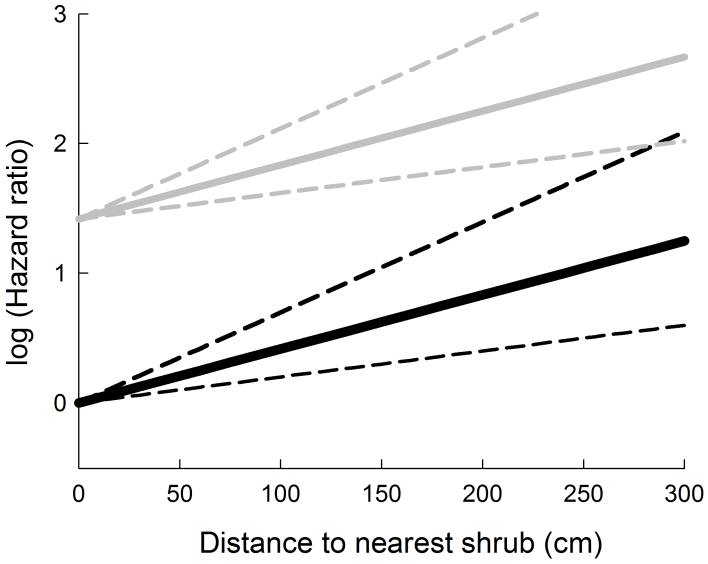

Figure 4. Predicted variation in the log hazard ratio for winter mortality as a function of distance to nearest shrub for *P. sylvestris* seedlings planted at montane (black) and subalpine (grey) sites in the Eastern Pyrenees. Solid lines represent predicted models whereas shaded areas correspond to 95% confidence intervals.

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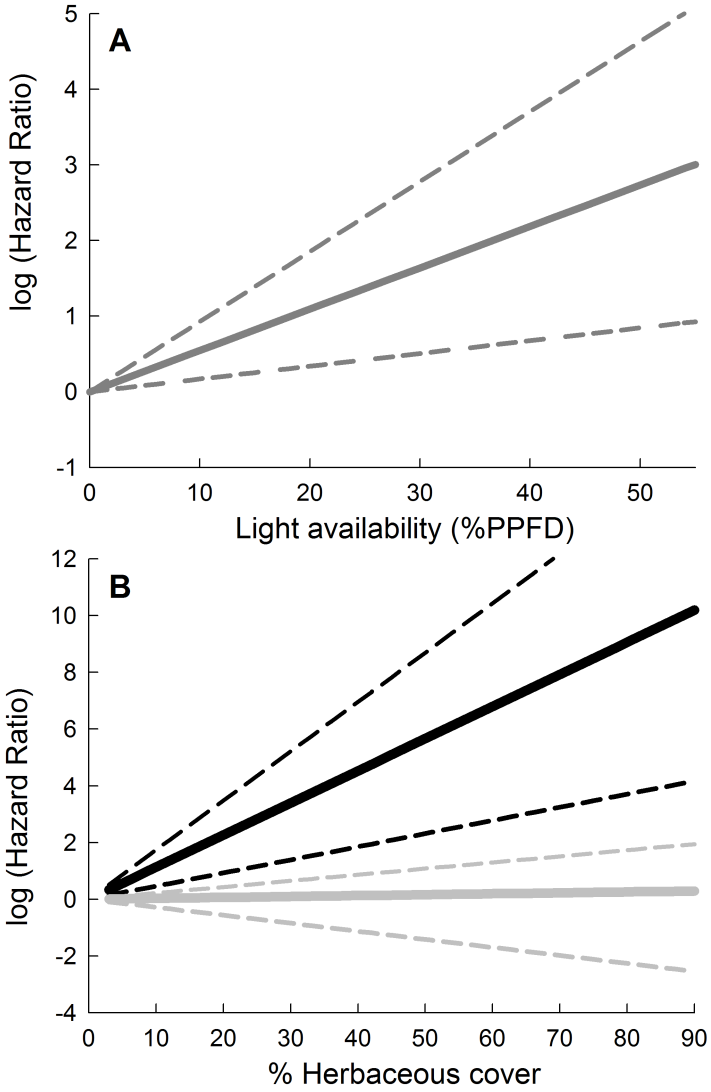

Figure 5. Predicted variation in the log hazard ratio for summer mortality as a function of (a) light availability and (b) percentage of herbaceous cover, for *A. alba* seedlings planted at montane (black) and subalpine (grey) sites in the Eastern Pyrenees. In (a), no significant effect of site was detected, and pooled data for both sites are represented in dark grey. Solid lines represent predicted models whereas shaded areas correspond to 95% confidence intervals.

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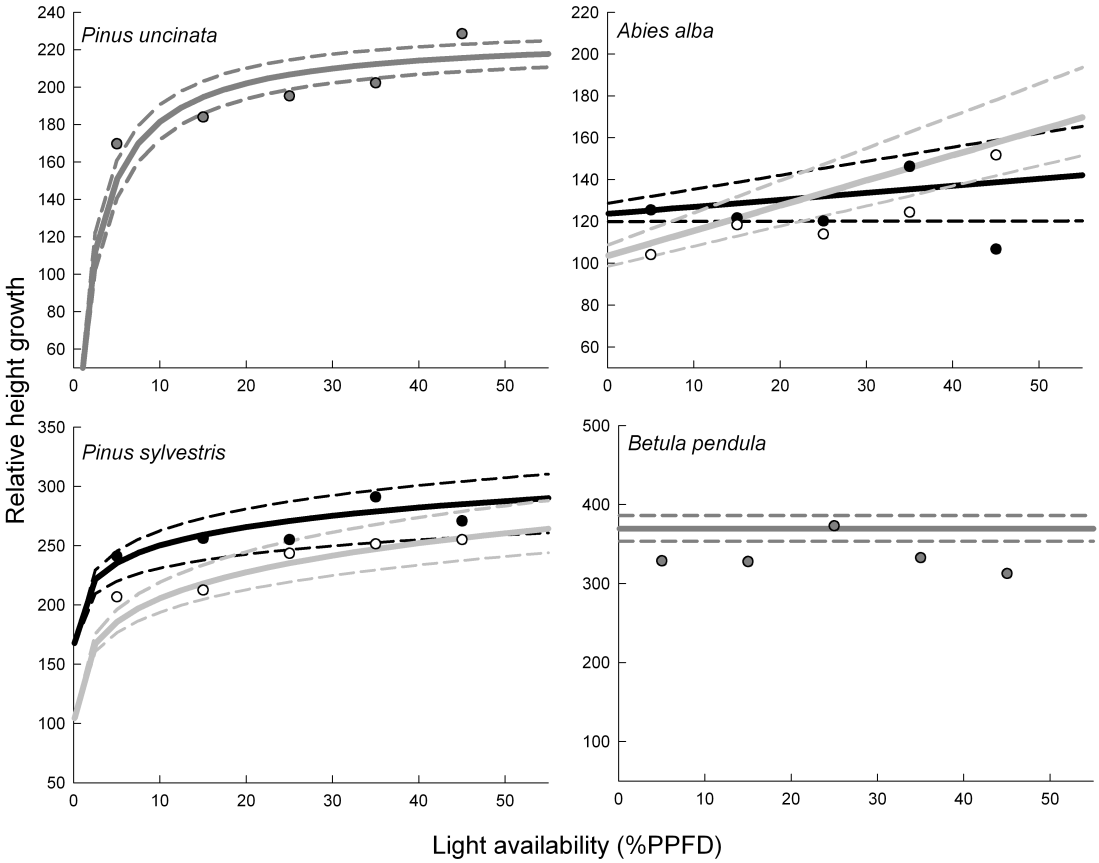

Figure 6. Predicted variation in height as a function of initial height and light availability for seedlings of the 4 studied species planted at montane (black) and subalpine (grey) sites in the eastern Pyrenees. When no effect of elevation was predicted, data were pooled together, and symbols are represented in dark grey. Solid lines represent predicted models whereas shaded areas correspond to 2-unit support intervals. Horizontal lines indicate lack of effect of the predictive variable for that species, and are shown for comparative purposes.

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TABLES

Table 1. Main abiotic and biotic characteristics of the studied stands

Variable	Montane sites	Subalpine sites
Latitude (N) / Longitude (E)	42º19'/ 1º43'	42º18' / 1º42'
Elevation (m a.s.l.)	1550	1955
Aspect/Slope (degrees)	NE / 39	NE / 53
Bedrock	Limestone	Limestone
Mean annual/summer temperature (ºC)	7.4 / 14.8	4.9 / 11.7
Total annual/summer precipitation (mm)	992 / 271	1118 / 327
Thornthwaite Index[1]	70.3	120.7
Length of the growing season[2] (days)	194	147
Mean Summer Maximum Temperature (ºC)	21.0	17.3
Mean Winter Minimum Temperature (ºC)	-3.4	-4.6
Dominant species[3]	Ps, Pu, Bp	Pu, Aa, Bp
Light availability (%PPFD)	19.3 ± 9.8 [2.8-55.1]	23.9 ± 13.3 [5.4-58.6]
Herbaceous Cover (%)	39.1 ± 23.1 [0-95]	51.1 ± 30.6 [0-100]
Distance to nearest shrub (cm)	56.5 ± 45.8 [10-350]	118.9 ± 76.3 [20-430]

Values for light availability, herbaceous cover, and distance to nearest shrub are means ± SD (n=286). Values in brackets are minimum and maximum observed values. The number of decimal positions indicates precision of the variable when measured.

[1] Calculated as the ratio between precipitation and potential evapotranspiration (Thornthwaite et al., 1957)

[2] Calculated as in Körner and Paulsen (2004)

[3] Listed for each site in decreasing order of dominance: Pu: *Pinus uncinata*; Aa: *Abies alba*; Ps: *Pinus sylvestris*; Bp: *Betula pendula.*

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Table 2. Summary of the models predicting seedling height as a function of microsite conditions and initial height for seedlings of four species of trees planted at two experimental sites in the Eastern Pyrenees. For each species and explanatory variable, the AIC of the best-fit model is provided for all seedlings pooled together (AIC_P) and separated into two groups (montane vs. subalpine, AIC_S)

Height	Model	AIC_P	AIC_S	R^2
Pinus uncinata				
Light	MM	2113.58	2123.75	0.33
Herb. cover	Lin	2136.17	2141.73	0.21
Null	Null	2207.46	2201.72	0.12
Abies alba				
Light	Lin	1669.49	1673.84	0.41
Herb. cover	Lin	1676.75	1679.01	0.30
Null	Null	1688.31	1688.16	0.25
Pinus sylvestris				
Light	Pow	2067.94	2055.57	0.36
Herb. cover	Lin	2076.28	2063.71	0.22
Null	Null	2085.66	2078.33	0.18
Betula pendula				
Null	Null	1771.06	1775.33	0.22

Factors are ranked from highest to lowest support according to AIC_P. For each species, only models with stronger empirical support than the null model (i.e. an AIC_P at least two units lower) are provided. Models are: Lin = linear; Exp = exponential, Pow = power, MM = Michaelis-Menten; see Appendix C for details on the equations. Lower AIC_S values than AIC_P values indicate stronger empirical support for separated data than for pooled data, i.e. an elevational effect.

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Table 3. Absolute and relative height growth at the end of the study period for seedlings of four species of trees planted at two experimental sites (montane and subalpine) in the Eastern Pyrenees. Absolute growth is expressed as average annual growth, and relative growth is annual growth relative to the initial state.

Species	Abs. height growth (mm·y-1)		Rel. height growth	
	Montane belt	Subalpine belt	Montane belt	Subalpine belt
Betula pendula	76.23 ± 4.44 a	69.73 ± 5.45 a	**0.381 ± 0.024 a**	**0.305 ± 0.027 a**
Pinus sylvestris	40.76 ± 1.91 b	34.98 ± 2.14 b	**0.289 ± 0.018 b**	**0.232 ± 0.016 b**
Pinus uncinata	30.48 ± 1.71 c	30.28 ± 2.04 b	0.283 ± 0.021 b	0.267 ± 0.021 b
Abies alba	16.48 ± 1.10 d	13.98 ± 1.18 c	**0.207 ± 0.016 c**	**0.160 ± 0.016 c**

Values are means ± SE. Values with the same letter indicate lack of significance between species. Values in bold indicate significant differences in relative growth between sites for a given species ($P < 0.05$).

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Post-print version. The final version of this article can be found at:

Ameztegui A, Coll L (2013) Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. Forest Ecology and Management 303: 25-34. DOI: https://doi.org/10.1016/j.foreco.2013.04.011

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